

ON THE BIOLOGY OF THE MESOGASTROPOD TRICHOTROPIS CANCELLATA HINDS, A BENTHIC INDICATOR SPECIES

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The observations on the mesogastropod, *Trichotropis cancellata* Hinds, with which the paper is concerned, were made during a period of some ten weeks in the summer of 1959 spent at the Friday Harbor Laboratory of the University of Washington, Seattle. They were supplemented by examination of further samples of living animals later that year in Seattle and during the early months of 1960 when working at the Hopkins Marine Station, Pacific Grove.

This research was not premeditated. It arose out of interest in an animal never previously encountered by the author. Thus, while a variety of most interesting points regarding ciliary feeding, protandric hermaphroditism, adaptation to a restricted range of bottom conditions and the mode of evolution of mesogastropod limpets were disclosed, no attempt could be made to probe deeper than was possible by examination of the living animal, although a few points have been confirmed and conclusions strengthened by subsequent sectioning of fixed material. But it is hoped that this general study may stimulate more detailed work. Particularly desirable would be a histological and experimental study of the protandric reproductive system over the two-year life span postulated in this paper. More precise information, to be obtained by means of grab samples, about the precise distribution of this species in relation to bottom substrates could also be most informing.

It is a pleasure to record thanks to colleagues of the summer season of 1959 at Friday Harbor, especially to Dr. Dixy Lee Ray and to Dr. R. L. Fernald who also sent additional samples of *Trichotropis* to Pacific Grove during February and March, 1960. Mr. Jefferson Gonor kindly reported on animals left in aquarium tanks at Friday Harbor and sent samples of these animals. Dr. J. Connell and Mr. G. Bakus identified species of barnacles and sponges which live on the shells of *Trichotropis*. At Pacific Grove every facility needed was supplied by the Director, Dr. L. R. Blinks, and members of his staff. The figures which illustrate this paper have been prepared by the author's research assistant, Miss J. I. Campbell. Grateful acknowledgment is also made to the United States Educational Commission in the United Kingdom for award of a Fulbright Travel Grant and to the Carnegie Trust for the Universities of Scotland for a grant towards expenses while working at Pacific Grove.

SYSTEMATIC POSITION

The genus *Trichotropis* Broderip and Sowerby 1829 is one of 10 genera in the Family Trichotropidae which, with the Capulidae and the Calyptraeidae, con-

stitutes the Superfamily Calyptraeacea (Thiele, 1931). But, as will later be shown, relationship to the Capulidae is certainly much closer than to the Calyptraeidae. Species of *Trichotropis* possess a thin shell covered by a relatively very thick periostracum which is thrown into the characteristic rows of long bristles (Fig. 1) which are responsible for the common name of these hairy-shells. This periostracum soon wears away apically when the underlying calcareous layer speedily becomes eroded.

Abbott (1954) in his account of American Molusca lists four species from northern seas: *T. borealis* Broderip & Sowerby which ranges from the Arctic to British Columbia and to Maine (also to northern Europe), *T. cancellata* Hinds from the Bering Sea to Oregon, *T. bicarinata* Sowerby from the Arctic to Alaska and to Newfoundland, and *T. insignis* Middendorff from Alaska to northern Japan. Thus, while all occur in the North Pacific only two species also inhabit the Atlantic.

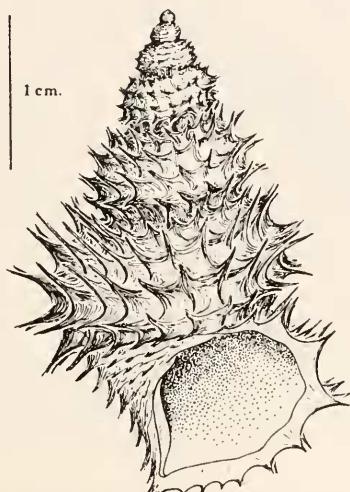


FIGURE 1. *Trichotropis cancellata*, empty shell showing characteristic spiral rows of periostracial spines.

SHELL AND INTACT ANIMAL

Shell

Both Oldroyd (1924), who quotes the description of Hinds from the zoology of the voyage of H.M.S. *Sulphur*, and Abbott (1954) give an account of the shell of *T. cancellata*. It is that of a typical mesogastropod with height about double the basal diameter, and with a well pointed spire. The deeply separated whorls each bear four or five spirally running keels across which run the rows of axial ribs which give the characteristic cancellated appearance. The shell attains greater lengths than appear previously to have been recorded, up to 42 mm. and with as many as 7 whorls. The aperture is rounded (Fig. 1) with a very short canal, and in a well grown, non-eroded shell is only about one-third the length of the shell. The flexible, lamellar operculum fits closely into the aperture.

The spines are composed entirely of periostracum, each consisting of many

parallel plates forming local extensions of the general periostracum which is formed in this way. The spines are roughly triangular, almost half as wide as they are long. Both the number of rows of spines and the length of these increases with the size of the shell, e.g. from 10 rows of maximum length 1.6 mm. in a shell 2.5 cm. long to 14 rows of maximum length 2.5 mm. in one 3.2 cm. long.

The shell grows by a series of obviously sudden bursts, as indicated by the conspicuous presence of areas of almost pure white shell in sharp contrast to the darker yellow or brownish older areas which are also usually overgrown with encrusting organisms (see later). A well marked flange marks the boundary between new and old areas. The relative degree of increase represented by any such burst of shell growth decreases with age and size; thus shells of lengths 1.4, 1.8, 2.7 and 3.3 cm. may recently have added approximately 1.3, 1.1, 0.5 and 0.3 whorls to the shell.

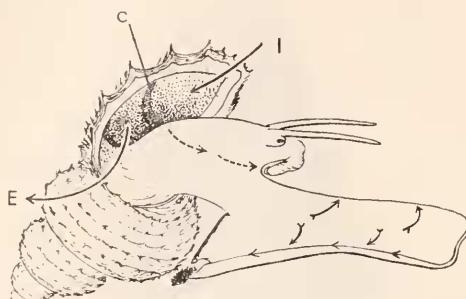


FIGURE 2. *T. cancellata*, youngest individual collected (shell length 5 mm.) before appearance of penis, with head and foot fully extended. Inhalant (I) and exhalant (E) currents, created by enlarged ctenidium (C), indicated by large arrows, route of collected food particles to mouth indicated by broken arrows, cleansing currents on surface of foot by feathered arrows, waste material accumulating at hind end below operculum.

The unusual bulk of the periostracum is indicated by the fact that the shell retains its form after complete decalcification. In three shells of between 2.7 and 3.4 cm. long so treated, the percentage by dry weight of non-calcareous matter was between 4.1 and 4.9. The great extent of the periodic bursts in shell growth may well be due to this unusually high content of periostracum, the material of which is rapidly secreted while the calcareous layers of the shell are more slowly and more continuously extended and thickened. The periodic "shoots" by which bivalves such as *Pinna* (Yonge, 1953b) increase the shell are also initially largely of protein although in this case composed almost entirely of the conchiolin matrix of the outer, prismatic layer of the shell valves.

Despite its thickness, the periostracum is soft and it is rare to find a shell of any size in which the spire is not eroded. The calcareous layers so exposed are often extensively bored into and superficially channelled by a variety of organisms including sponges and small annelids, and probably algae. Unless covered over by the many larger organisms which attach themselves to the shell (see later), the apical whorls may be completely lost. It seems doubtful whether the shell could provide adequate shelter for the animal for longer than the two years which, for other reasons, are postulated as the life span in this species.

Intact animal

When examined in sea water under a binocular microscope, the animal readily emerges from the shell, revealing the general appearance of head and foot shown in Figure 2 which represents the smallest animal collected, only 5 mm. long and immature without trace of the penis (the only such individual found). The foot is long and, at any rate until the urge to move as far as possible upwards has been

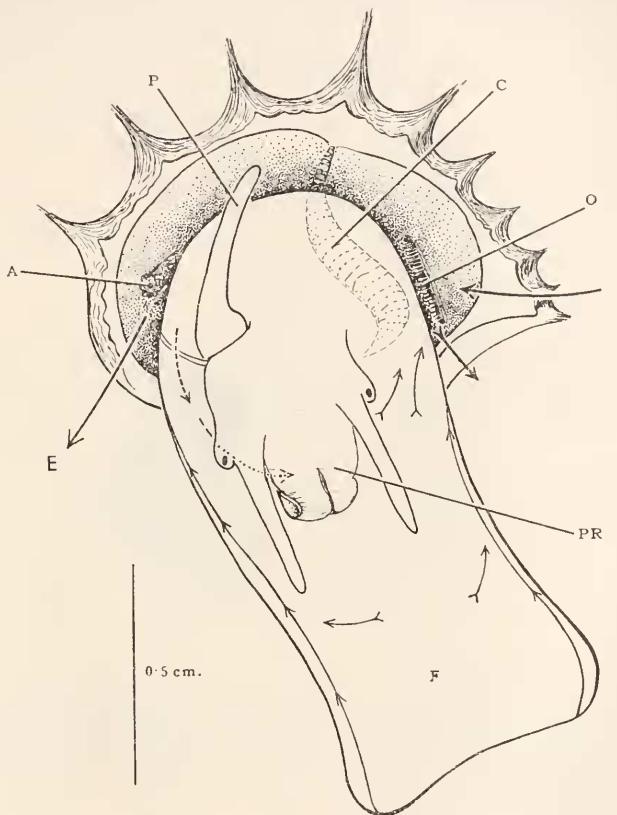


FIGURE 3 *T. cancellata*, animal extended out of shell showing foot, head and opening into mantle cavity. A, anus; C, ctenidium (viewed largely through body); F, foot; O, osphradium; P, penis; PR, proboscis. Plain arrows, respiratory and feeding current; broken arrows, food current to mouth (passing under right tentacle); feathered arrows, rejection currents.

satisfied, very active. It is ciliated dorsally, material being carried laterally into the grooves which run backward from either side of the opening of the pedal gland which extends across the broad anterior end of the foot. Cilia in these grooves beat posteriorly so that sediment from the foot collects in mucous masses at the posterior end of the foot beneath the operculum (see arrows in Figure 2).

The head bears a pair of long tentacles, each with an eye on a rounded basal protuberance. As described by Graham (1954) in *T. borealis* and precisely as

in *Capulus ungaricus* (Yonge, 1938), the mouth lies at the end of a short grooved suboral proboscis. Powerful ciliary tracts coming from the floor of the mantle cavity extend round the right side of the head and carry particles to the proboscis (Figs. 2 and 3). This curls under and may move to one side or the other but certainly not invariably to the right as Graham states occurs in *T. borealis*. Without further evidence from the ctenidium, it was immediately possible to confirm Graham's statement that species of *Trichotropis*, like the allied *Capulus* (Orton, 1912; Yonge, 1938), are ciliary feeders.

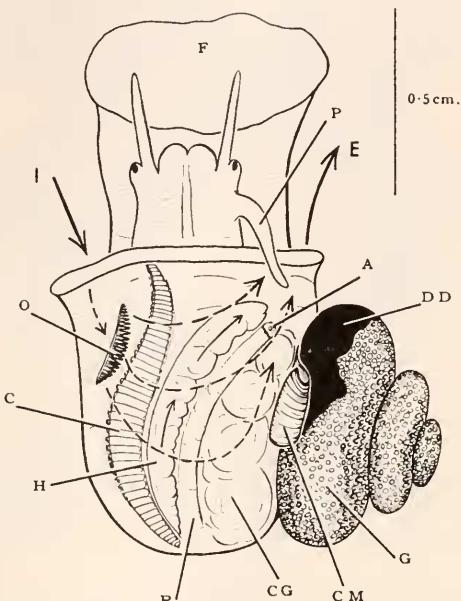


FIGURE 4. *T. cancellata*, animal removed from shell with pallial organs shown *in situ*. CG, capsule gland; CM, columellar muscle; DD, digestive diverticula; G, gonad; H, hypobranchial gland; R, rectum. Other lettering as before. Broken arrows indicate course of water currents in the mantle cavity, solid arrows, currents along surface of hypobranchial gland.

The appearance of an adult animal viewed from above as it emerges from the shell is shown in Figure 3. Here the large penis (P), *invariably present* in all but the very smallest animals, lies at the base of the right tentacle and running into it is the open seminal groove. Over this passes the food current from mantle cavity to proboscis (PR). The anterior end of the ctenidium (C) (also shown in Figure 2) appears about the middle of the roof of the mantle cavity. To the left of this (right as viewed in the figure) the dark line of the long osphradium (O) is just visible deeper within the cavity, while well to the right side the lobed margins of the anus (A) can be seen. A very powerful inhalant current (I) enters by way of the very short canal on the left side of the shell aperture; the exhalant current (E) leaves on the right, carrying with it faeces, renal products and mucus-entangled sediment from the hypobranchial gland.

FEEDING AND DIGESTION

1. Mantle cavity

In correlation doubtless with its food-collecting function, the mantle cavity is unusually deep and the contained organs, otherwise those of a typical mesogastropod, are enlarged. Their general disposition when revealed after removal of the animal from the shell, first with the mantle intact and then with this opened along the right side, is shown in Figures 4 and 5, respectively. Omitting for the time being reference to the reproductive ducts, the organs of the pallial complex—osphradium (O), ctenidium (C) and hypobranchial gland (H)—followed by the rectum (R) lie, roughly parallel to one another from left to right, along the roof. As indicated by the broken arrows in Figure 4, the water current created by the lateral cilia on the ctenidial filaments passes over each of these in turn.

Osphradium. This organ is unusually large, almost half the length of the enlarged ctenidium. It is monopectinate (not bipectinate as Graham describes it as being in *T. borealis*) and consists of some 30 filaments coming off on the right of the axis. Each is deeply pigmented on the frontal surface and cilia carry particles across its surface towards the ctenidium. The position of the osphradium is typical, *i.e.*, in the region where the heavier particles carried in the inhalant stream fall out of suspension. It also marks the point of division between the ciliary currents which carry heavier particles across the floor of the cavity and those which are retained in suspension and are carried across the roof. The significance of this is discussed below.

Ctenidium. This extends in a somewhat sinuous curve from near the margin of the mantle cavity into almost the deepest recesses where it terminates just short of the renal pore (RP) which discharges into the exhalant current. It is a typical pectinibranch ctenidium with the axis on the left and a single row of filaments, each with its lateral tracts of current-producing cilia supported beneath by a skeletal rod (Yonge, 1938, 1947). In a large animal (of shell length 3.5 cm.) the ctenidium consists of some 130 filaments. Small at the ends, these attain a length of 4 mm. in the middle of the series. Moreover, like the filaments of other ciliary feeding mesogastropods, *e.g.* species of *Capulus*, *Vermetus* and *Crepidula* (Yonge, 1938) or of *Struthiolaria* (Morton, 1951), they are not triangular but elongate, being about four times as long as they are broad. Thus without any great increase in the respiratory surface, the tracts of lateral cilia are elongated and so the volume of the inhalant current augmented. Particles suspended in this current when it reaches the ctenidium are largely intercepted by the frontal and abfrontal cilia which line their near and further edges. These cilia convey particles, some of them edible, to the tips of the filaments. In life these hang down towards the floor of the cavity on to which the particles are transferred by the agency of groups of terminal cilia some 30μ long. As indicated by the arrows in Figure 5, all such particles are then carried round the right side of the head and thence to the under side of the proboscis (see broken arrow in Figure 3).

Hypobranchial gland. This lobulated structure occupies a considerable area down the middle of the roof of the cavity. On mechanical stimulation it secretes copious mucus and is covered with cilia which beat towards the opening of the cavity. Consequently the finest particles which pass between the ctenidial fila-

ments are here entangled in mucus and carried to the right side of the cavity for extrusion in the exhalant current (see Figure 4).

Ciliary currents. Apart from the lateral cilia on the ctenidial filaments which create the respiratory current, all cilia in the mantle cavity of Mollusca were primitively concerned with removing particles of sediment, *i.e.*, with cleansing to prevent fouling of the respiratory chamber. In the Prosobranchia (Yonge, 1938) these cleansing currents are divisible into the following three groups:

- A. Cilia on the margin of the inhalant region which convey the largest and heaviest particles which settle immediately to the exterior via the *inhalant* opening.
- B. Cilia on the floor of the mantle cavity which carry medium-sized particles which settle deeper within the cavity across to the right where they are carried out through the exhalant opening.
- C. Cilia on the frontal and abfrontal edges of the ctenidial filaments and on the surface of the hypobranchial glands, all on the roof of the cavity, in which the finest particles are collected and entangled in mucus and then extruded via the exhalant opening.

In ciliary-feeding mesogastropods these currents are modified so that to greater or less extent the collected material is passed to the mouth, *i.e.*, the currents become concerned with feeding. No new currents appear. Thus in *Vermetus novae-hollandiae* currents B and C only are diverted to carry food to the mouth but in *Crepidula fornicata* and *Capulus ungaricus* all three currents are so modified (Yonge, 1938).

In *T. cancellata* current A is present and unmodified (see feathered arrows in Figures 3 and 5). But the position with regard to B and C is unusual and interesting. Owing to the length and position (along the roof) of the ctenidial filaments these will form, as indicated in Figure 4, an effective partition between a narrower left inhalant, and a larger right exhalant, chamber. It follows that all but particles ejected by current A will reach the gills where all but the most minute will be carried down on to the floor of the cavity and so into current B which is solely concerned with food collection. But the finest particles which pass between the filaments on to the surface of the hypobranchial gland are there consolidated in mucus and extruded from the cavity in current C which is thus unmodified in function.

There is *no* anterior passage of particles along the free margin of the ctenidium, with or without an associated food groove along the floor of the cavity, as there is in the other ciliary-feeders mentioned. Nor in *Trichotropis* is the ctenidium directed to the right; indeed, there is the minimum of change apart from enlargement of the ctenidium and its movement to a mid-dorsal position together with elongation of the individual filaments. Nevertheless the particles collected in current B, *i.e.*, by the sole agency of the ctenidium, do appear to represent the only source of food. Graham (1954) does not describe the currents in the mantle cavity of *T. borealis*, noting only (p. 131) that particles from the inhalant current "fall on to and travel across the floor of the mantle cavity" and so are conveyed to the proboscis. But later he states (p. 140) that the trichotropids "may gather food with their proboscis as well as collect it out of the water current maintained

through the mantle cavity." But in *T. cancellata*, of which many hundreds of specimens were observed, there is certainly no evidence that the proboscis is ever in a position to take in any material other than what is passed to it in current B from the ctenidium by way of the floor of the mantle cavity.

The position of the osphradium in relation to the three currents will be noted. Like the ctenidium, this organ is enlarged, and surely because of the increased current produced and so greater entry of sediment into the mantle cavity. The chemo-receptive powers which the osphradium comes to possess in the carnivorous neogastropods have no relevance to the needs of a ciliary-feeder and the contention (Yonge, 1947) is here reiterated that the osphradium is primarily a tactile organ

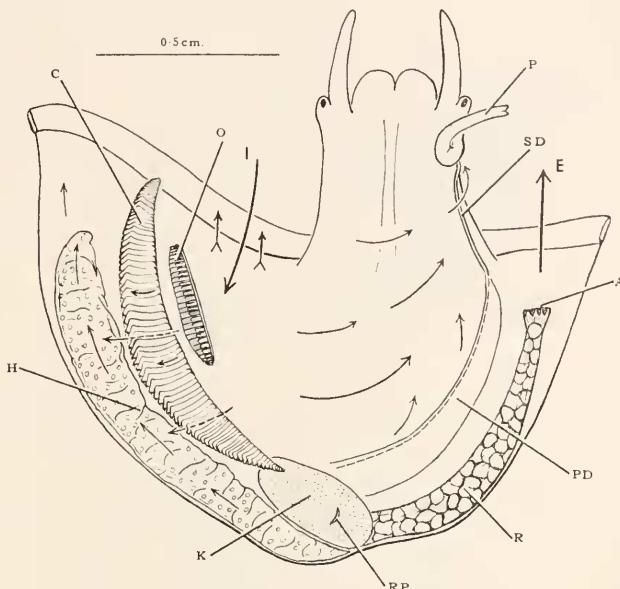


FIGURE 5. *T. cancellata*, anterior end with mantle cavity opened along right side. K, kidney; PD, pallial reproductive duct; RP, renal pore; SD, sperm duct (open groove). Other lettering as before. Rejection currents on left floor of mantle cavity (feathered arrows), feeding currents on right leading over sperm duct to proboscis under head.

concerned with estimation of the amount of sediment which enters the all-important respiratory chamber. For that reason it is enlarged in animals such as the trichotropids in which the inhalant current, and so the incoming content of sediment, is increased.

2. Alimentary canal

Foregut. As described by Graham (1954) for *T. borealis*, cilia within the groove of the proboscis carry mucus-laden food masses up to the mouth where they are grasped by the radula and passed back through the buccal cavity. There are no jaws. A pair of bag-like salivary glands opens at the base of the cavity by short and wide ducts. Graham states that those of *T. borealis* secrete an almost pure mucus for the lubrication of the radula.

The primitive prosobranch oesophagus has been described by Graham (1939) as consisting of an anterior oesophagus, on the roof of which runs a pair of folds enclosing a ciliated dorsal food groove, a mid-oesophagus which bears lateral pouches in which digestive enzymes are secreted and a posterior and purely conducting region. He states that the glandular mid-oesophagus is absent in style-bearing prosobranchs.

In *T. cancellata* both anterior oesophagus, with its powerfully ciliated dorsal food groove, and a posterior oesophagus with ridged and ciliated walls are present. But as Professor Graham, who has compared sections of *T. cancellata* with his of *T. borealis*, agrees, oesophageal glands are much better developed in the former and have a characteristic epithelium absent in *T. borealis*. He raises the question as to whether this should be reflected in the classification, but this must be left for subsequent workers to decide.¹ What is certain is that the animal possesses both oesophageal glands and a crystalline style. Indeed, apart from the presence of the oesophageal glands, conditions throughout the gut generally in *T. cancellata* closely resemble those in *Capulus ungaricus* (Graham, 1939, 1954).

Stomach. When this is opened the first thing visible is the style. In an animal 3.5 cm. long, this is some 9 mm. long and about 1 mm. in diameter. A great deal of material is usually found embedded in the head which normally consists of a soft brownish mass. There may also be a thick central core of such material. While initially firm enough, the style very rapidly softens, which must explain Graham's failure to find it in *T. borealis* where he states there is a style-sac but with no style.

The appearance of the stomach when opened is shown in Figure 6. Owing to the effects of torsion, the oesophagus (OE) opens at what is now the posterior end of the stomach and the intestine (I) leaves at the anterior extremity. As noted (but not figured) by Graham (1954) for *T. borealis* and figured by him in *Capulus ungaricus*, two large ducts from the digestive diverticula (D) open one beside the entrance of the oesophagus, the other at the base of the intestinal groove (IG). The area between is finely ridged with cilia beating towards the intestinal groove. Cilia beat away from the openings of the ducts but these are mobile and food particles are probably drawn in when they dilate. In *T. borealis* the diverticula contain two types of cell, one digestive and the other probably excretory (Graham, 1954). Precisely similar cells are present in the diverticula of *T. cancellata*.

The oesophageal end of the stomach is rounded with a well developed gastric shield (GS) against which the head of the style was seen to bear when initially exposed. Ciliary tracts converge to carry material entering from the oesophagus in the head of the style where it will be rotated and mixed with its enzymes. The style-sac (SS) has the usual character, being covered with a glistening surface of dense cilia and separated from the intestinal groove by the major and minor typhlosoles. The directions of the various ciliary currents are indicated by the arrows in Figure 6. Cilia on the major typhlosole (MA) push the style towards the gastric shield, those on the general surface rotate it; on the minor typhlosole (MI) and in the intestinal groove (IG) they are concerned with moving rejected material, with much mucus, into the intestine.

¹ See Taxonomic Addendum by Robert Robertson (p. 179).

Intestine and rectum. These regions, which run very directly from stomach to anus, are solely concerned with consolidation of the faeces. They are ciliated throughout with some muscle, especially in the rectal regions where peristalsis occurs. Graham (1954) states that mucous glands occur at both ends of the intestinal region in *T. borealis* but with other gland cells, probably secreting a protein which forms the outer covering of the faecal pellets, present in the middle regions. The oval pellets so formed in *T. cancellata* may be separate or united in chains by a common outer covering. Passing in single file through the intestine, they frequently congregate in masses in the rectum (Fig. 5). The anal opening (A) is lobed.

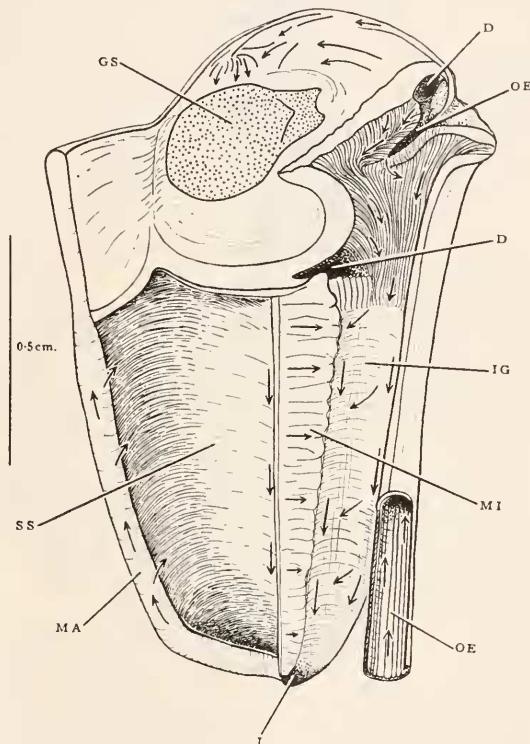


FIGURE 6. *T. cancellata*, stomach opened laterally. D, ducts into digestive diverticula; GS, gastric shield; I, opening into intestine (mid-gut); IG, intestinal groove; MA, MI, major and minor typhlosoles; OE, oesophagus; SS, style sac. Arrows indicate course of ciliary currents.

According to Graham (1939), the primitive prosobranch possessed mid-oesophageal glands which, with the apparent exception of *Adeorbis*, have been lost where a style is present, this being correlated with continuous feeding, largely on vegetable matter (Yonge, 1932). However, another exception is certainly *T. cancellata* where both glands and style are well developed, although not, according to Graham (1954), in *T. borealis*. While this difference clearly demands further examination and perhaps some change in classification, it is probably

significant that *T. cancellata* (and doubtless related species) has a less specialized ciliary feeding mechanism than any other mesogastropod. The acquisition of a style may thus be relatively recent with the primitive oesophageal glands, possibly no longer secreting a protease, still retained.

REPRODUCTIVE SYSTEM

A most striking fact about *T. cancellata* is that all but a few very small and obviously immature individuals appear on external examination to be males. Of a series of over 600 animals, ranging in length from 1.4 to 4.1 cm., initially examined during July and August, all possessed a well developed penis. One specimen 5 mm. long (Fig. 2) had no penis and up to mid-September seven other immature specimens between 0.6 and 1.2 cm. long were collected showing various stages in the development of the penis starting with a minute papilla. But no adult examined, including very extensive samples received at Seattle in December and others at Pacific Grove in February and March, was without a large penis.

This apparent anomaly was resolved by examination of the gonad and reproductive ducts when, even on macroscopic examination, it became obvious that, apart from these few obviously immature specimens, *all* animals were in process of change from the male to the female condition or were, despite the presence of the penis, fully functional females.

The reproductive system (Fig. 7) is not otherwise unusual. The gonad (G) occupies the summit of the twisted visceral mass and from it the convoluted gonadal portion of the reproductive duct (GD) extends over the surface of the digestive diverticula to the base of the mantle cavity. By way of a short intervening renal section it is there continued as a wider and open pallial section which runs diagonally across the floor of the mantle cavity (Fig. 5, PD).

In young animals the gonadal follicles are clear green in colour and obviously testicular, but in older animals they become cream-coloured with increasingly large opaque areas denoting the formation of the large, yolk eggs. But all this time the convoluted gonoduct continues to be full of motile sperm. These macroscopic observations were later confirmed by sections.

During the early, male, phase the pallial gonoduct consists of a deep but open groove which makes connexion, by way of a wide, slit-like opening, with the seminal groove (SD) which leads to the penis. But in older animals in which the gonad is changing from testis to ovary, this region of the gonoduct hypertrophies with formation of the extensive glandular areas which, as shown in Figures 4 and 7, come to occupy the right side of the mantle roof and extend over the rectum. When fully formed this represents the capsule gland (see Fretter, 1946, for details concerning the reproductive ducts in mesogastropods). The degree of its formation is the only external indication of change of sex and even this involves removal of the animal from the shell.

These very general observations indicate that *T. cancellata* is a protandrous hermaphrodite and confirm the similar conclusions reached by Graham (1954) in his study of *T. borealis*. In a relatively small sample he had both small males and large females, the former with and the latter without a penis. Apparently the collection was made near to the time of copulation and spawning. Thus the Trichotropidae resemble the Calyptaeidae and also *Capulus* (the position in the

allied but parasitic *Thyca* is obscure) in which the process of sex change has been fully described by Giese (1915). Protandry also occurs in *Hipponix*, belonging to the related Amaltheidae (Yonge, 1960).

But in all cases hitherto described the penis is lost in the female phase. The sequence of events in species of *Crepidula* is well known while collections of *Calyptarea fastigiata* made at the same time as those of *T. cancellata* contained

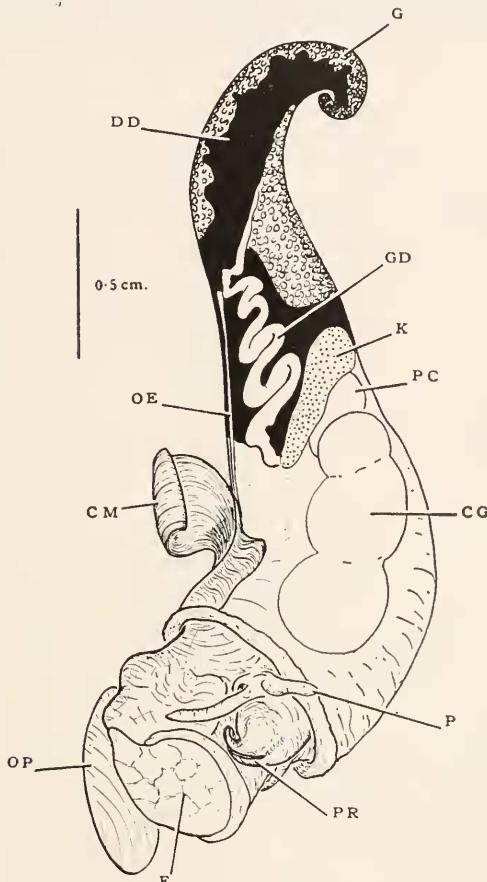


FIGURE 7. *T. cancellata*, animal removed from shell showing major organs. GD, gonadal reproductive duct; OP, operculum; PC, pericardium. Other lettering as before.

small males with shell diameter about 1 cm. and large females of twice that size; the former possessed the conspicuous penis found in this genus, the latter had lost all trace of this and were spawning. Even in the sessile *Hipponix* the smaller animals have a conspicuous penis lacking in the larger individuals which are all females (Yonge, 1960).

T. cancellata is the first such protandrous hermaphrodite to be described in which the penis is retained throughout life. As already noted, every individual of a large collection examined in December possessed a penis. It was then assumed

that this organ would be lost before the animals became functional females in the spring. Dr. R. L. Fernald (personal communication) had already found that spawning occurs in March and April. But all members of large final samples of *T. cancellata* flown from Friday Harbor to Pacific Grove between the middle of February and the end of March, and which ranged in length from 1.5 to 4.2 cm., possessed a well developed penis. Over 100 individuals were removed from their shells and the reproductive organs examined. It was then possible, as outlined in Table I, to separate them into five groups, one of males (M) and four of females (F_1 to F_4).

TABLE I

*Sexual condition of 108 specimens of *T. cancellata* examined between 28.ii.61 and 3.iii.61*

Group	Size range in cm.	State of gonad	Gonadal duct	Capsule gland	Penis	Condition	No. of individuals
M	1.5-2.4	Empty testis (clear yellow)	Distended with sperm	No trace	Present	Male	7
F_1	2.5-4.1	Full ovary (opaque yellow)	No sperm	Developed, some capsules forming	Present	Female unfertilized	22
F_2	2.1-4.0	Full ovary	Much sperm	Capsules fully formed	Present	Females ready to spawn	43
F_3	3.5-4.2	Half-empty ovary	Full of eggs	Capsules fully formed	Present	Females spawning	6
F_4	2.8-4.2	Empty and degenerating (red)	Empty or few eggs	Usually fully discharged	Present	Females spent	30

The population thus consisted of a few ripe males (few doubtless because so much less likely to be retained in the dredge bag and to be noted when the catch was sorted) and numerous females which could be divided into four groups, (F_1) not quite ripe, (F_2) ripe and fertilized, (F_3) spawning, (F_4) spent. With one exception to be mentioned later, the females showed no evidence of recent growth and the soft periostracal spines were worn away, whereas the males had wide areas of recently formed shell with intact spines. As already noted, the state of the capsule gland is an excellent index of maturity in the female phase. After a period of steady development over the autumn and winter, it becomes an opaque white but with no sign of secreted capsules, the condition in group F_1 . Gelatinous capsules then begin to be secreted (F_2); these are next liberated in spawning (F_3) and finally the gland is left yellowish and empty (F_4).

After change from the male phase, the gonad gradually becomes distended with yellow eggs (F_1); these round off prior to ovulation (F_2), following which they pack the gonadal duct where they have an average diameter of some 250 μ (F_3). The gonad is finally left flaccid and empty, apart from a few residual eggs and some reddish pigment (F_4).

The gonadal duct is distended with sperm in the active male phase and continues to contain sperm certainly well into the autumn and beginning of winter. But prior to maturity in the female phase, the duct appears empty (F_1) but then becomes filled again with sperm (F_2), presumably following copulation. After ovulation it is distended with eggs (F_3) and after completion of spawning, is empty apart from a few undischarged eggs (F_4).

From its first appearance when the shell is under 1 cm. long, the penis is present, continuing to enlarge with the growing animal. Possible reasons are the long retention of sperm within the gonadal duct or, more probably, the continuation, revealed by sections, of sperm production. In a few cases some sperm were being produced in March when the animals were ready to lay eggs. A detailed study of the gonad throughout life would be rewarding.

Although small animals, later confirmed to be males, were placed with numerous females in an aquarium tank at Pacific Grove where they appeared to live well and where some females later spawned, copulation was never observed. However, the absence of sperm in some unspawned females (F_1) and its presence in others (F_2) indicates that many females had already copulated, presumably before they were dredged at Friday Harbor. However, the position is complicated by the fact that, as reported by Mr. Jefferson Gonor, specimens left over the winter in the aquarium tanks at the Friday Harbor Laboratory also produced apparently fertile egg capsules and there seems some doubt as to whether males were present. This also requires further examination. It is possible that late sperm produced at the end of the second year may permit self-fertilization. Although Wyatt (1960) found no evidence of self-fertilization in the Calytraeidae, conditions may well be different in *Trichotropis*.

Beginning on March 7, six animals spawned on the glass sides of the tanks at Pacific Grove. They remained immobile during this process, the individual capsules being applied to the glass by the foot and arranged spirally, although all in the one plane. The greatest number of capsules produced by any animal was 26 over a period of 12 days, the final diameter of the mass being 1.7 cm. Additions (between 1 and 4) were always made at night, so that possibly light inhibits a process which may therefore be much quicker in nature.

When laid the individual capsules are round and flat, with a diameter of about 4.5 and a height of 3.5 mm. New capsules are attached peripherally, the spawn forming a rounded mass with each capsule assuming the shape of a rounded pentagon. Apart from the attached surface, which is a little thinner, the wall is about $60\ \mu$ thick. The yolk-laden and fertilized eggs, some already cleaving when first observed, are contained in a thin membrane which is possibly formed in the gonadal duct. The number of contained eggs varies very greatly, from perhaps a hundred to an occasional empty capsule. But there was little opportunity for following development which did not appear to proceed normally. This would best be observed in naturally deposited capsules.

The capsules of *T. borealis* from Greenland have been described and figured by Thorson (1935). They are rounded and between 2.75 and 4.75 mm. in basal diameter and are deposited on empty bivalve shells in clusters of only 2 to 4. Up to 13 embryos were found in each capsule but this was in mid-July with development almost completed. All capsules had an irregular exit hole through which young had already escaped. These emerged in the crawling stage and possessed peculiar conchiolin membranes running in spirals around the whorls. Thorson also describes the capsules, up to 13 in a group, and the larvae of *T. conica* which are attached to sabellid tubes.

In *T. cancellata* the spawning period certainly covers the months of March and April as observed by Dr. R. L. Fernald. It may well start in mid-February.

while Mr. Gonor found a few specimens still depositing capsules in the tank at Friday Harbor as late as May 13. The three months from mid-February probably represent the full extent of the breeding season around Friday Harbor.

After spawning the great majority of animals die. In some cases the operculum has already become partially resorbed, while macroscopic examination of the tissues of the visceral mass immediately after spawning reveals widespread degeneration in both ovary and digestive diverticula. Although only a few of the animals received from Friday Harbor actually spawned, and even then development did not appear to be normal, the majority of the others only lived a few weeks or even days. Death in many cases had been preceded by ovulation, the ovary being in the same flaccid, degenerating state as in animals that had spawned. In some, death was obviously due to parasitism by small reddish trematode redia but usually it appeared to be natural. After ovulation the life span would seem normally to be completed. On May 13, Mr. Gonor reported the presence of 198 dead and only 36 survivors of the population which had been left in the tank at Friday Harbor. Some of the latter were spawning and others may possibly have been males. It is just possible that a few females which do not spawn may survive into a third year of life. One animal 3.2 cm. long, showing recent growth of shell, was encountered in March. This was a female and very dubiously ready to spawn. But it should be noted that at the end of two years the shell is usually so much eroded, especially at the apex, that survival for a further year would be impossible.

LIFE-HISTORY

From the information already recorded the course of the life-history of *T. cancellata* may be deduced, the salient facts being indicated in Figure 8. Spawning occurs between mid-February and mid-May with production of animals which grow relatively rapidly and begin to assume male characters during the late summer. This is indicated by the absence of a penis in the specimen (Fig. 2) 0.5 cm. long taken in late July and its presence in increasing size in animals up to 1.2 cm. long found in late August and mid-September. Growth continues over the winter, with accompanying enlargement of the penis and development of the testis, so that at the end of the first year of life animals, now between 1.5 and 2.4 cm. long (M in Table I), are functional males.

After copulation change to the female condition begins, the ovary slowly developing but with growth unchecked until mid-summer when animals reach almost the maximum recorded length (4.1 cm.). While change in the gonad is obvious, change in the pallial gonoduct (although doubtless beginning much earlier) does not become apparent macroscopically until the autumn when the capsule gland becomes an obvious feature in the mantle cavity. Over the second winter there is little or no evidence of further growth but both the ovary and the capsule gland become fully formed so that, fertilized by the one-year-old males, the animals can function as females at the end of the second year (*i.e.*, in the second spring as shown in Figure 8).

The long spawning period produces a great range in size. Thus the 610 animals measured in August, 1959, ranged in length from 1.4 to 4.1 cm. with a well marked unimodal peak between 2.8 and 3.3 cm. There was no evidence of

any but a single year class (the immature male individuals being excluded). All of these animals had a fully developed penis and a yellow gonad. The 101 mature females reported on in Table I ranged in size from 2.5 to 4.2 cm. It is possible that some of the latest spawned individuals may not become functional females at the end of the second year and continue for a further year to spawn, if the condition of the shell permits them to survive so long, at the end of the third year. But for the great majority of individuals the duration of life appears to be two years, the animals functioning as males at the end of the first, and as females at the end of the second, year.

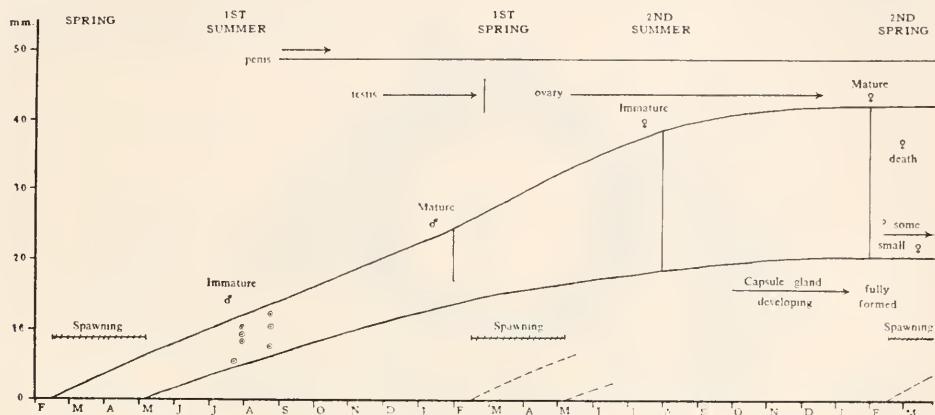


FIGURE 8. *T. cancellata*, probable course of life history graphically displayed.
For details see text.

HABITS

These can be epitomized in one sentence, *T. cancellata* always moves as high as possible and then remains quiescent. Placed on the bottom of aquarium tanks the animals crawl actively until they encounter a wall or any vertical or partly vertical surface. They then move up this to the highest available point. In the aquarium this is normally the water level where they congregate, layers deep should numbers be great. Where the surface above water level is permanently wet they will even climb several inches out of water. They remain in this position indefinitely. The few animals on the bottom which fail in their wanderings to encounter a vertical surface usually die within a few days, apparently owing to fouling of the mantle cavity with sediment from the circulating water which there accumulates.

Despite the presence of eyes, upward movement is not influenced by light, as many animals climb the dark, as the illuminated, surfaces of a tank. There is never any horizontal movement towards (or away from) a source of illumination. Movement appears to be a simple negative reaction to the pull of gravity. Having reached the highest available point—even although above water level, a state of affairs never encountered in nature by these sublittoral animals—movement ceases and is not resumed unless the animal is dislodged. Adhesion is maintained by the partly distended foot with the head and tentacles pushed as far forward as possible

and the mantle cavity open. In this position, with the shell slightly raised and the mantle cavity fully open, water circulation is maintained as shown in Figure 9. The animal respires and collects suspended matter from an inhalant current largely free from sediment.

On a muddy substrate the animals immediately begin to flounder and soon become immobilized in a mass of mucus-laden mud. Even on mixed shell gravel and mud, movement is greatly hampered. *T. cancellata*, and doubtless other species of the genus, demands a firm substratum for locomotion and clear water for feeding.

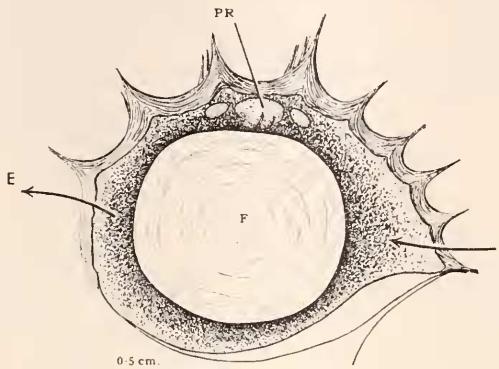


FIGURE 9. *T. cancellata*, appearance when attached to glass, quiescent and feeding.
Lettering as before.

Probably no gastropod shell is so richly covered with such a variety of attaching organisms. A considerable paper could be written on the subject of this associated fauna and flora. Both the spinous covering on the shells and the habits of life encourage settlement. Within the shelter of the spines the surface is usually covered with a forest of small hydroids and encrusting polyzoons, and with chains of diatoms. A variety of small errant polychaetes and of copepods and other small crustaceans feed on the debris which collects between the spines. A small gastropod with a smooth white shell, probably a species of *Odostomia*, is not uncommon and usually in pairs.

In certain areas the shell of *T. cancellata* may be covered by a variety of large associates which in total bulk, or even singly, may have a greater volume than the shell to which they are attached (Fig. 10). These include the sponge, *Ectyodoryx parasitica* (de L.) (= *Myxilla parasitica* (Lambe)) which forms irregular yellowish masses as large as the shell; the sabellid *Eudistylia vancouverensis* (Fig. 10B) up to 4 cm. long and usually with a colony of a species of the naked two-tentacled hydroid, *Proboscidactyla*, encircling the opening of the tube; or the acorn barnacle, *Balanus balanus pugetensis* Pilsbry, which is sometimes as large as the shell and often with smaller individuals attached to a larger one. Most striking of all are the simple ascidians, notably the flat-topped *Chelyosoma productum* (Fig. 10A), of which as many as five, all larger than the shell, may be fastened to one *T. cancellata* which is completely obscured by them. Almost as common are *Styela gibbsii*, rounded and some 2.5 cm. in diameter,

Pyura haustor (Fig. 10B) which is up to 4 cm. long, and *Boltenia villosa* with a stalked and rounded body some 2.5 cm. across. A single shell may carry representatives of all of these ascidians, together with the sabellid, so that the resultant mass may be many times the volume of the shell to which all are directly or indirectly attached (Fig. 10).

While the hairy shell certainly provides an admirable micro-habitat for many small encrusting and browsing animals, the extent of attachment by larger as well as smaller animals gives confirmatory information about the habits *in situ* of *T. cancellata*. To permit so much settlement and enable the attaching animals to grow so large, the snails must live fully exposed and move about very little. Aquarium observations are thus confirmed.

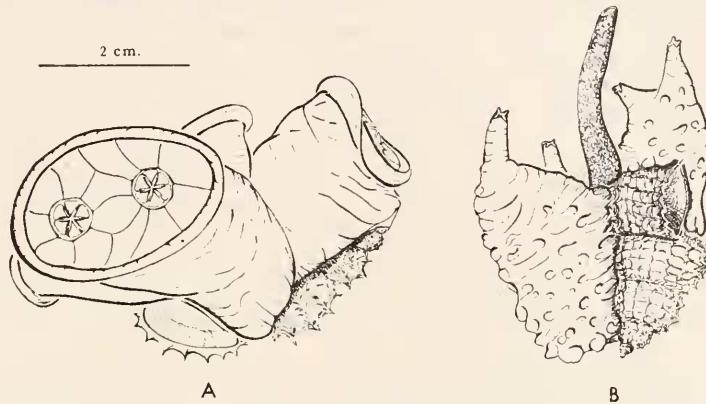


FIGURE 10. *T. cancellata* with attached organisms. A, shell largely obscured by four individuals of the simple ascidian, *Chelyosoma productum*; B, shell carrying two individuals of the ascidian, *Pyura haustor*, and between these a specimen of the sabellid worm, *Eudistylia vancouverensis*.

These snails may be envisaged as moving as high as possible on the irregular surface of the shelly bottom they inhabit, then remaining motionless with mantle cavity open for feeding and respiration. The shell with its dense coating of bristles will then present the maximum of well-protected settling surface. Movements of the foot appear sufficient to prevent the larger attaching organisms from growing over the shell aperture. Dislodgement by water movements or by the activities of larger animals will provoke renewed upward movement. Because the attaching sponges—tunicates, sabellids and barnacles—are also suspension feeders, the habits of the snail are of major advantage to them.

DISCUSSION

Two matters remain for final discussion. First there is the significance of *T. cancellata* as a biological indicator of a certain type of substrate, second the light thrown by consideration of this, and related, species on the probable course of evolution of mesogastropod limpets.

The complicated topography of the water passages between the San Juan Islands, together with the great variations in depth and in the local force of tidal currents,

produce a range of bottom conditions possibly unsurpassed in any similar area. The scouring action of tidal currents in restricted passages produces the hard bottom occupied by a characteristic epifauna of largely sessile animals such as hydrocorallines and *Balanus nubilis*; maximum deposition on the bottom of deep pits or of sheltered embayments produces a soft mud substratum inhabited by suitably adapted members of the infauna. Every possible gradation between these two extremes appears to occur.

Amongst ciliary suspension feeders, many bivalves burrow in the mud while beds of *Modiolus modiolus* cover extensive areas of relatively firm bottom. In restricted areas of pure shell gravel *Glycymeris subobsoleta* is effectively the sole inhabitant, being the only bivalve which can exploit this habitat. But in certain areas where bottom currents are so powerful as to allow the unstable accumulation of little more than mounds of empty, usually bivalve, shells, an environment is produced offering unique opportunities to *T. cancellata*. No bivalve (or gastropod) can burrow here, while the substrate is too unstable for the establishment of beds of *Modiolus*. This instability also prevents successful settlement of sessile suspension feeders. But *T. cancellata* can move about freely, making inevitable progress to the highest available point where its ciliary feeding mechanism can function with maximum efficiency, the animal remaining motionless until dislodged. It then resumes upward movement. This unusual combination of mobility with a stationary habit while feeding perfectly fits this animal for life on a firm but unstable substratum. It also, as already described, renders it an ideal object of settlement by a wide variety of epifaunal suspension feeders.

The statement by Thorson (1935) that the egg capsules of *T. borealis* are laid on empty shells indicates that this species occupies a similar habitat which is probably true for all species of the genus. *T. cancellata* does extend, although in diminishing numbers, on to bottoms of mixed shell and gravel although the precise limits of its distribution can only be determined by grab samples. As an indicator of bottom conditions, this species can take its place with other sublittoral mesogastropods such as *Turritella communis*, a ciliary feeder which burrows in a bottom of stiff mud with some gravel (Graham, 1938; Yonge, 1946) and *Aporrhais pes-pelecani*, a deposit feeder which burrows in muddy gravel, and *A. serrciana* found somewhat deeper within bottoms of softer mud, the two species hardly overlapping (Yonge, 1937).

In the Mesogastropoda the limpet form and habit has been evolved in the families Capulidae (including *Capulus* and *Thyca*), Calyptraeidae (including *Calyptroca* and *Crepidula*) and Amaltheidae (including *Hipponix*). Unlike the universal habit in the far more numerous archaeogastropod limpets, none feeds by radular scraping but by ciliary currents (*Capulus*, *Calyptroca*, *Crepidula*), by the proboscis (*Hipponix*) or parasitically (*Thyca*). This is associated with a general tendency towards a sessile habit finding ultimate expression in *Hipponix antiquatus* which becomes permanently fixed early in post-larval life (Yonge, 1953a, 1960) and in the parasitic *Thyca*. The nature of the reproductive system, which involves internal fertilization and formation of complex egg capsules, raises problems absent in archaeogastropod limpets such as *Acmaea* or *Patella* where gametes are discharged freely into the sea. The difficulties presented to a sessile animal by the need for internal fertilization are largely met by the occurrence of

protandrous hermaphroditism, with the animal still active in the early male phase (*Capulus*, *Calyptrea*, and some species of *Crepidula*), by the formation of chains (*C. fornicate* and other species of *Crepidula*), or by the presence of an unusually large penis (*Hipponix*).

This study of *Trichotropis* throws some light on how these mesogastropod limpets may have evolved. The pectinibranch ctenidium has been enlarged to form an organ of feeding as well as of respiration (though with modification of only one of the three cleansing currents in the mantle cavity). The animal is passive when feeding. In other words, evolution of a ciliary feeding mechanism and of a passive habit presumably preceded evolution of the limpet form which is that best fitted for sedentary existence. It provides maximum surface of attachment and minimum surface against which dislodging forces can act. Conditions in *Trichotropis* further reveal that protandry may also precede the assumption of the limpet form, although accompanying assumption of some measure of the limpet habit. It may reasonably be assumed that the mesogastropod limpets, amongst the most interestingly modified members of an order exhibiting unparalleled capacity for adaptive radiation, evolved from animals very similar in form and habits to *Trichotropis*.

TAXONOMIC ADDENDUM

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The anatomical and functional differences between *Trichotropis cancellata* Hinds and *T. borealis* Broderip & Sowerby reported above by Yonge are in accord with a very recently proposed taxonomic grouping, in which one of these species is placed in a different genus. T. Habe (1961, Coloured Illustrations of the Shells of Japan (II). Osaka, Japan (publ. Hoikusha). P. 36 and appendix pp. 13–14) has renamed *Ariadna* Fischer, 1864 (*non* Audouin in Savigny, 1826) *Ariadnaria*, ranking it as a genus. The type species of *Ariadnaria* Habe and of *Ariadna* Fischer is *Trichotropis borealis*, by monotypy (Fischer). *T. cancellata* can be grouped in *Turritropis* Habe (1961, *ibid.*) because conchologically it much more closely resembles the type species of this taxon [*Trichotropis cedo-nulli* A. Adams] than it does the type of *Trichotropis*, s.s. [*T. bicarinata* (Sowerby)]. *Ariadnaria* and *Turritropis* may be ranked as genera distinct from *Trichotropis*, s.s., or grouped as subgenera within *Trichotropis*, s.l.

SUMMARY

1. *Trichotropis cancellata* Hinds is a member of the Trichotropidae which, with the Capulidae and Calyptraeidae, constitutes the Superfamily Calyptraeacea. As in other species of the genus, the shell is covered with unusually thick periostracum prolonged into characteristic spiral rows of spines. Older shells are always deeply eroded apically.

2. The mantle cavity possesses the typical organs of a mesogastropod. Particles collected by the enlarged, but not otherwise specialized, ctenidium are carried by ciliary currents, representing modification of only one out of three groups of

cleansing tracts, under the right side of the head to the grooved proboscis. Enlargement of the monopectinate osphradium is to be associated with greater intake of sediment in the augmented inhalant current.

3. The gut is unusual in possessing both a glandular region in the oesophagus and a crystalline style. The former, primitive, structure is usually lost when a style is present. This provides further evidence of the relatively recent adoption of the ciliary feeding habit.

4. Like other Calyptraeaceae, *T. cancellata* is protandric. The penis first appears in animals over 0.5 cm. long. Spawning (at Friday Harbor) is probably from mid-February to mid-May, the animals functioning as males when one year old and between 1.5 and 2.4 cm. long.

5. During the second year, change to the female condition occurs with modification of the pallial reproductive duct to form a capsule gland, the eggs now produced by the gonad being deposited in gelatinous capsules when the animals are two years old and reach a maximum length of 4.2 cm. The great majority, if not all, then die.

6. The process of egg laying, although not of copulation, has been observed.

7. Unlike allied animals, including *T. borealis*, the penis is retained and enlarges throughout life. This may be due to long retention of sperm in the gonadal duct, more probably to continuation, sometimes until egg-laying, of some production of sperm in the gonad. There is evidence that self-fertilization may occur.

8. Habits involve the simple process of moving as high as possible and then remaining quiescent while feeding on suspended matter drawn in with the increased inhalant current. Only when dislodged is activity resumed. Despite the presence of eyes, habits appear uninfluenced by light.

9. *T. cancellata* is thus admirably adapted for life on a firm but unstable substrate of dead, largely bivalve, shells. It flounders on soft substrates. Probably no gastropod shell is so richly covered with such a diversity of attaching organisms. Both the spinous covering and the habits encourage settlement of organisms up to the size of tube worms, barnacles and ascidians, the total bulk of which may greatly exceed that of the shell.

10. *T. cancellata* is an indicator of a restricted type of bottom condition. Much may be learnt from it about the manner in which the limpet form and habit has been acquired in the Mesogastropoda. Assumption of the habit of life, represented here by ciliary feeding and protandry, clearly precedes that of the limpet form.

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